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Research Article

# Two new species of *Penicillium* (Eurotiales, Aspergillaceae) from China based on morphological and molecular analyses

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## Abstract

*Penicillium* is a large and significant genus of fungi, exhibiting widespread distribution across diverse substrates. Ongoing taxonomic and nomenclatural revisions have led to an annual increase in the number of newly described species. This study described two new *Penicillium* species, i.e., *P. lentum* and *P. tibetense*, discovered in China. They have been identified and characterized through morphological examination and both single gene and multigene phylogenetic analyses. Based on these analyses, *P. lentum* was classified within the section *Brevicompacta*, while *P. tibetense* was placed in the section *Lanata-Divaricata*. Both species exhibited the morphological features typical of their respective sections. *Penicillium lentum* is characterized by restricted growth with dense colonies on agar media and predominantly generates terverticillate conidiophores. *Penicillium tibetense* demonstrates rapid growth on media and has vigorous growth on CYA at 30 °C, producing biverticillate conidiophores. Comprehensive descriptions and detailed illustrations of these new species were presented. A morphological comparison between the new species and their closely related taxa was provided.

**Key words:** Aspergillaceae, DNA barcodes, section *Brevicompacta*, section *Lanata-Divaricata*, taxonomy

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## Introduction

*Penicillium* is widely distributed across various substrates, primarily in soil, as well as in the atmosphere, food, plant tissues, and other environments. Several species possess considerable value for human applications in food production, biocontrol, and biotechnology. For instance, *P. sclerotiorum* exhibits antagonistic activity against certain plant pathogens, demonstrating potential as a biocontrol agent (Jahan et al. 2024). The food industry utilizes *P. nalgiovense* as starter cultures for dry-fermented sausages (Ludemann et al. 2010). The capability of certain species to synthesize pigments has prompted the evaluation of these species for the production of highly stable and safe natural pigments (Morales-Oyervides et al. 2020). Nevertheless, mycotoxins generated by specific species present a significant risk to human and animal health (Nielsen et al. 2017). Notably, patulin exhibits multiple toxicities, including genotoxicity and immunotoxicity, and is predominantly produced by *P. expansum* and *P. griseofulvum* (Bandoh et al. 2009; Puel et al. 2010; Tannous et al. 2014).

Link (1809) introduced the generic name *Penicillium*, which is classified in the family Aspergillaceae. Traditional taxonomy of *Penicillium* primarily relied on morphological characters, including colony diameter, texture, conidial color, and conidiophore branching patterns. However, the variability in morphology has presented substantial challenges in accurately identifying novel species, frequently resulting in the erroneous classification of new isolates under known species (Visagie et al. 2016). Conversely, contemporary taxonomy adopts a polyphasic strategy that incorporates morphological, extrolite, genetic, and multigene phylogenetic data (Visagie et al. 2014). Houbraken et al. (2020) delivered the most comprehensive update on the genus *Penicillium* based on a phylogenetic approach combined with phenotypic, physiologic, and extrolite data. This study recognized 483 species and introduced a novel series classification, which is deemed highly predictive of potential functional traits (Houbraken et al. 2020). Subsequently, Visagie et al. (2024b) applied GCPSR (Genealogical Concordance Phylogenetic Species Recognition) and phylogenetic analyses to reassess the list of *Penicillium* species published up to 31 December 2022, resulting in an updated count of 535 species. An additional 100 species of this genus were described from 1 January 2023 to 31 December 2024 (Ansari et al. 2023; Crous et al. 2023; da Silva et al. 2023; Khuna et al. 2023; Li et al. 2023; Liu et al. 2023; Tan 2023; Tan and Shivas 2023, 2024; Tan et al. 2023, 2024a, 2024b; Wang et al. 2023; Zhang et al. 2023; Araújo et al. 2024; Crous et al. 2024; Liang et al. 2024; Lima et al. 2024; Nóbrega et al. 2024; Song et al. 2024; Visagie et al. 2024a, 2024c; Zhang et al. 2024). The increase in species numbers in recent years indicates the possibility of numerous undiscovered *Penicillium* species, and their biodiversity, ecological functions, and potential for resource development warrant further investigation.

During a comprehensive survey of *Penicillium* biodiversity in China, we found two isolates that could not be classified within existing species. In this paper, we compare these isolates with related species using multi-locus phylogenetic analyses and morphological character assessments. As a result, the isolates are described as species new to science. This study is expected to offer new perspectives on the diversity, function, ecology, and distribution of *Penicillium* members.

## Materials and methods

### Isolates

Soil samples were collected from the rhizosphere of plants in the Kangyu Tunnel, Tibet, China, while indoor dust samples were sourced from Beijing Forestry University, Beijing, China. To isolate the fungus, the samples were suspended in sterile water at a ratio of 1:10, vortexed to ensure homogeneity, and then diluted to $10^{-4}$ concentrations. Each of 100 µL from $10^{-2}$, $10^{-3}$, and $10^{-4}$ dilutions was spread on potato dextrose agar (PDA) and Martin medium with 50 ppm penicillin and 50 ppm streptomycin. The cultures were incubated at 25 °C for 5–7 days. Individual colonies were then picked from the plates and transferred to fresh PDA plates until pure cultures were obtained. Type specimens, preserved as dry cultures, were deposited in the Fungarium (HMAS), Institute of Microbiology, Chinese Academy of Sciences, while ex-type strains, maintained as living cultures, were stored at the China General Microbiological Culture Collection Centre (CGMCC).

## Morphological studies

Morphological observations of colonies were conducted under strictly standardized conditions, encompassing media preparation, inoculation technique, incubation parameters, and description methods (Visagie et al. 2014). Colony characters and diameters were recorded from cultures grown on Czapek yeast autolysate agar (CYA), malt extract agar (MEA), yeast extract sucrose agar (YES), dichloran 18% glycerol agar (DG18), and creatine sucrose agar (CREA) at 25 °C for 7 days. Additional CYA plates were incubated at 30 and 37 °C. Color names and codes adhered to the book "Color Standards and Color Nomenclature" (Ridgway 1912). Ehrlich reaction was employed to assess the production of indole metabolites; a violet ring observed within ten min was deemed a positive result, while other color changes were interpreted as negative (Lund 1995; Houbraken et al. 2016).

For light microscopic observations, slides were prepared from cultures grown on MEA, and phenol glycerin solution was used as mounting fluid, with cotton blue staining if necessary. In addition, a field emission scanning electron microscope (Hitachi SU8010, Japan) was employed to examine microstructural characteristics. Agar blocks (3–4 mm × 3–4 mm) were fixed in 2.5% v/v glutaraldehyde at 4 °C for 8–12 hr, then washed three times for 10 min each with 0.1M phosphate buffer. Dehydration was performed with a gradient of ethanol (30, 50, 70, 95, and 100% v/v) for 10–20 min per step, followed by replacement with tert-butanol and ultimate vacuum freeze-dried and gold-sprayed for observation (Wei et al. 2024).

## DNA extraction, sequencing, and phylogenetic analyses

Colonies were cultivated on MEA plates for 5–7 days, and DNA extraction was conducted using the E.Z.N.A.® Fungal DNA Mini Kit (Omega Bio-Tek, Inc., United States). The internal transcribed spacer (ITS), beta-tubulin (*BenA*), calmodulin (*CaM*), and RNA polymerase II second largest subunit (*RPB2*) genes were amplified using primer pairs ITS1/ITS4 (White et al. 1990), Bt2a/Bt2b (Glass and Donaldson 1995), CMD5/CMD6 (Hong et al. 2006), and RPB2-5F/RPB2-7CR (Liu et al. 1999), respectively. Polymerase chain reaction (PCR) amplification followed Visagie et al. (2014). Sequencing reactions were performed by Sangon Biotech (Shanghai) Company Limited, China. DNAMAN software (Lynnon Biosoft) was used for the assembly and trimming of the Sanger chromatograms. Sequences were submitted to GenBank (www.ncbi.nlm.nih.gov).

Sequence similarity searches were conducted using the mega BLAST program of basic local alignment search tool (BLAST) within the NCBI core nucleotide database (core_nt). Comprehensive sequence datasets were compiled containing newly generated sequences alongside reference sequences sourced from GenBank (Table 1). Sequence alignments were performed using the ClustalW algorithm and subsequently manually edited using MEGA 11 (Tamura et al. 2021). The resulting multiple sequence alignments have been deposited in TreeBASE (submission number: 31847) (www.treebase.org). Phylogenetic trees were constructed based on the ITS, *BenA*, *CaM*, and *RPB2* genes as well as the concatenated sequences of the latter three genes. Phylogenetic analyses were conducted using both maximum likelihood (ML) and Bayesian Inference (BI). ML phylogenies were performed using IQtree v. 1.6.12 (Nguyen et al. 2015), including 1000 standard non-parametric boot-

**Table 1.** Strains of *Penicillium* used for phylogenetic analyses.

| Species | Strain | Substrate and origin | GenBank accession numbers | | | |
|---|---|---|---|---|---|---|
| | | | ITS | *BenA* | *CaM* | *RPB2* |
| *P. abidjanum* | CBS 246.67$^T$ | Soil, Ivory Coast | GU981582 | GU981650 | MN969234 | JN121469 |
| *P. alagoense* | URM 8086$^T$ | Leaves of *Miconia* sp., Brazil | MK804503 | MK802333 | MK802336 | MK802338 |
| *P. amphipolaria* | CBS 140997$^T$ | Soil, Antarctica | KT887872 | KT887833 | KT887794 | MN969177 |
| *P. annulatum* | CBS 135126$^T$ | Air sample, South Africa | JX091426 | JX091514 | JX141545 | KF296410 |
| *P. araracuaraense* | CBS 113149$^T$ | Leaf litter, Colombia | GU981597 | GU981642 | MN969237 | KF296414 |
| *P. astrolabium* | CBS 122427$^T$ | Grapes, Portugal | DQ645804 | DQ645793 | DQ645808 | JN406634 |
| *P. ausonanum* | CBS 148237$^T$ | Sediment of freshwater stream, Spain | LR655808 | LR655809 | LR655810 | LR655811 |
| *P. austrosinense* | CGMCC 3.18797$^T$ | Acidic soil, China | KY495007 | KY495116 | MN969328 | KY495061 |
| *P. bialowiezense* | CBS 227.28$^T$ | Soil under conifers, Poland | EU587315 | AY674439 | AY484828 | JN406604 |
| *P. bissettii* | CBS 140972$^T$ | Soil from spruce forest, Canada | KT887845 | KT887806 | KT887767 | MN969178 |
| *P. brasilianum* | CBS 253.55$^T$ | Herbarium exsiccata, Brazil | GU981577 | GU981629 | MN969239 | KF296420 |
| *P. brevicompactum* | NRRL 28139 | Stroma of a wood decay fungus, USA | AY484917 | DQ645795 | AY484825 | – |
| | CV1492 | Unknown, South Africa | JX091398 | JX091533 | JX141574 | – |
| | CBS 257.29$^T$ | Unknown, Belgium | AY484912 | AY674437 | AY484813 | JN406594 |
| *P. buchwaldii* | CBS 116980 | Wheat, United Kingdom | JX313163 | JX313181 | JX313147 | – |
| | CBS 116935 | Wheat, United Kingdom | JX313156 | JX313174 | JX313140 | – |
| | CBS 116929 | Wheat flour, Denmark | JX313152 | JX313170 | JX313136 | – |
| | CBS 117181$^T$ | *Hordeum vulgare*, Denmark | JX313164 | MN969374 | JX313148 | JN406637 |
| *P. camponoti* | CBS 140982$^T$ | Carpenter ants, Canada | KT887855 | KT887816 | KT887777 | MN969179 |
| *P. cataractarum* | CBS 140974$^T$ | Fallen nuts of *Carya cordiformis*, Canada | KT887847 | KT887808 | KT887769 | MN969180 |
| *P. coffeatum* | CGMCC 3.25152$^T$ | Soil, China | OQ870815 | OR051121 | OR051298 | OR051466 |
| *P. daleae* | CBS 211.28$^T$ | Soil under conifer, Poland | GU981583 | GU981649 | MN969251 | KF296427 |
| *P. echinulonalgiovense* | CBS 328.59$^T$ | Unknown, Japan | GU981587 | GU981631 | KX961269 | KX961301 |
| *P. excelsum* | DTO 357-D7$^T$ | Brazil nut shell, Brazil | KR815341 | KP691061 | KR815342 | MN969166 |
| | ITAL 7804 | Flowers, Brazil | KT749963 | KT749959 | KT749962 | – |
| *P. expansum* | CBS 325.48$^T$ | *Malus sylvestris*, USA | AY373912 | AY674400 | DQ911134 | JF417427 |
| *P. fengjieense* | CGMCC 3.25157$^T$ | Soil, China | OQ870765 | OR051156 | OR051333 | OR051489 |
| *P. fennelliae* | CBS 711.68$^T$ | Soil, Congo | JX313169 | MN969382 | JX313151 | JN406536 |
| *P. flaviroseum* | CGMCC 3.18805$^T$ | Acidic soil, China | KY495032 | KY495141 | MN969329 | KY495083 |
| *P. fructuariae-cellae* | CBS 145110$^T$ | Dried fruit of *Vitis vinifera*, Italy | MK039434 | KU554679 | MK045337 | – |
| *P. globosum* | CBS 144639$^T$ | Acidic soil, China | KY495014 | KY495123 | MN969330 | KY495067 |
| *P. griseoflavum* | CGMCC 3.18799$^T$ | Acidic soil, China | KY495011 | KY495120 | MN969331 | KY495064 |
| *P. griseopurpureum* | CBS 406.65$^T$ | Soil under *Pinus* sp., United Kingdom | KF296408 | KF296467 | MN969261 | KF296431 |
| *P. guaibinense* | CCDCA 11512$^T$ | Soil, Brazil | MH674389 | MH674391 | MH674393 | – |
| *P. guangxiense* | CBS 144526$^T$ | Soil, China | KY494986 | KY495095 | MN969332 | KY495045 |
| *P. hainanense* | CGMCC 3.18798$^T$ | Acidic soil, China | KY495009 | KY495118 | MN969333 | KY495062 |
| *P. infrabuccalum* | CBS 140983$^T$ | *Camponotus pennsylvanicus*, Canada | KT887856 | KT887817 | KT887778 | MN969181 |
| *P. jianfenglingense* | CGMCC 3.18802$^T$ | Acidic soil, China | KY495016 | KY495125 | MN969334 | KY495069 |
| *P. jinyunshanicum* | CGMCC 3.25162$^T$ | Soil, China | OQ870766 | OR051157 | OR051334 | OR051490 |
| *P. kongii* | AS3.15329$^T$ | leaf sample of *Cotoneaster* sp., China | KC427191 | KC427171 | KC427151 | – |
| *P. laevigatum* | CGMCC 3.18801$^T$ | Acidic soil, China | KY495015 | KY495124 | MN969335 | KY495068 |
| ***P. lentum*** | **CGMCC 3.28596$^T$ = B24** | **Indoor dust, Beijing, China** | **PQ643282** | **PQ519854** | **PQ519855** | **PQ519856** |
| *P. mariae-crucis* | CBS 271.83$^T$ | *Secale cereale*, Spain | GU981593 | GU981630 | MN969275 | KF296439 |
| *P. marykayhuntiae* | BRIP 74934a$^T$ | Soil, Australia | OR271913 | OR269446 | – | OR269440 |
| *P. neocrassum* | CBS 122428$^T$ | Grapes, Madeira | DQ645805 | DQ645794 | DQ645809 | JN406633 |
| *P. newtonturnerae* | BRIP 74909a$^T$ | Soil, Australia | OP903478 | OP921964 | OP921962 | OP921963 |
| *P. ochrochloron* | CBS 357.48$^T$ | Copper sulphate solution, USA | GU981604 | GU981672 | MN969280 | KF296445 |
| | DTO 189-A6 | Unknown, Japan | KC346347 | KC346324 | KC346341 | KC346318 |

| Species | Strain | Substrate and origin | GenBank accession numbers | | | |
|---|---|---|---|---|---|---|
| | | | ITS | *BenA* | *CaM* | *RPB2* |
| *P. olsonii* | CBS 232.60$^{T}$ | *Musa*, France | EU587341 | AY674445 | DQ658165 | JN121464 |
| *P. onobense* | CBS 174.81$^{T}$ | Soil, andosol, Spain | GU981575 | GU981627 | MN969281 | KF296447 |
| *P. panissanguineum* | CBS 140989$^{T}$ | Soil near termite mound, Tanzania | KT887862 | KT887823 | KT887784 | MN969182 |
| *P. paraherquei* | CBS 338.59$^{T}$ | Soil, Japan | AF178511 | KF296465 | MN969285 | KF296449 |
| *P. pauciramulum* | CGMCC 3.25164$^{T}$ | Soil, associated with nest of Formicidae, China | OQ870726 | OR051111 | OR051288 | OR051457 |
| *P. pedernalense* | CBS 140770$^{T}$ | *Litopenaeus vannamei*, Ecuador | KU255398 | KU255396 | MN969322 | MN969184 |
| *P. penarojense* | CBS 113178$^{T}$ | Leaf litter, Colombia | GU981570 | GU981646 | MN969287 | KF296450 |
| *P. piscarium* | CBS 362.48$^{T}$ | Cod-liver oil emulsion, Germany | GU981600 | GU981668 | MN969288 | KF296451 |
| *P. pulvillorum* | CBS 280.39$^{T}$ | Acidic soil, United Kingdom | AF178517 | GU981670 | MN969289 | KF296452 |
| | CBS 275.83 | Rye grain, Spain | GU981601 | GU981671 | KC346336 | KF296423 |
| *P. rolfsii* | CBS 368.48$^{T}$ | Fruit of *Ananas sativus*, USA | JN617705 | GU981667 | MN969294 | KF296455 |
| *P. roodeplaatense* | DTO 444-C8 | Soil, South Africa | OR819195 | OR820176 | OR820180 | OR820186 |
| *P. rotoruae* | CBS 145838$^{T}$ | *Pinus radiata* timber stake in ground contact, New Zealand | MN315103 | MN315104 | MN315102 | MT240842 |
| *P. rubriannulatum* | CGMCC 3.18804$^{T}$ | Acidic soil, China | KY495029 | KY495138 | MN969336 | KY495080 |
| *P. salamii* | CBS 135391$^{T}$ | Salami, Italy | HG514431 | HG514437 | HG514432 | MN969160 |
| *P. simplicissimum* | CBS 372.48$^{T}$ | *Secale cereale*, Spain | GU981588 | GU981632 | MN969297 | JN121507 |
| *P. singorense* | CBS 138214$^{T}$ | House dust, Thailand | KJ775674 | KJ775167 | KJ775403 | MN969138 |
| *P. skrjabinii* | CBS 439.75$^{T}$ | Soil, Russia | GU981576 | GU981626 | MN969299 | EU427252 |
| *P. soliforme* | CGMCC 3.18806$^{T}$ | Acidic soil, China | KY495038 | KY495147 | MN969337 | KY495047 |
| | NN072390 | Acidic soil, China | KY495019 | KY495128 | KY494959 | KY495072 |
| | NN072399 | Acidic soil, China | KY495022 | KY495131 | KY494962 | KY495074 |
| *P. spathulatum* | CBS 117192$^{T}$ | Mouldy chestnut (*Castanea* sp.), France | JX313165 | MN969400 | JX313149 | JN406636 |
| *P. spinuliferum* | CBS 144483$^{T}$ | Acidic soil, associated with *Litchi chinensis*, China | KY495040 | KY495149 | MN969338 | KY495090 |
| *P. stangiae* | URM 8347$^{T}$ | Soil, Brazil | MW648590 | MW646388 | MW646390 | MW646392 |
| *P. stolkiae* | CBS 315.67$^{T}$ | Soil, South Africa | AF033444 | JN617717 | AF481135 | JN121488 |
| *P. subfuscum* | CBS 147455$^{T}$ | Soil, South Africa | MT949907 | MT957412 | MT957454 | MT957480 |
| *P. subrubescens* | CBS 132785$^{T}$ | Soil of *Helianthus tuberosus* field, Finland | KC346350 | KC346327 | KC346330 | KC346306 |
| *P. subrutilans* | CGMCC 3.25174$^{T}$ | Soil, China | OQ870816 | OR051137 | OR051314 | OR051479 |
| *P. svalbardense* | CBS 122416$^{T}$ | Glacial ice, Svalbard | GU981603 | DQ486644 | KC346338 | KF296457 |
| *P. taii* | CGMCC 3.25176$^{T}$ | Soil, China | OQ870778 | OR051170 | OR051347 | OR051496 |
| *P. tanzanicum* | CBS 140968$^{T}$ | Soil near termite mound, Tanzania | KT887841 | KT887802 | KT887763 | MN969183 |
| *P. terrarumae* | CBS 131811$^{T}$ | Soil contaminated by heavy metals, China | MN431397 | KX650295 | MN969323 | MN969185 |
| | CS23-08 | Unknown, China | OQ870751 | OR051141 | OR051318 | OR051481 |
| *P. tularense* | CBS 430.69$^{T}$ | Soil under *Pinus ponderosa* and *Quercus kelloggii*, USA | AF033487 | KC427175 | JX313135 | JN121516 |
| | CBS 431.69 | Soil under *Pinus ponderosa* and *Quercus kelloggii*, USA | JX313167 | AY674433 | JX313134 | – |
| *P. vanderhammenii* | CBS 126216$^{T}$ | Leaf litter, Colombia | GU981574 | GU981647 | MN969308 | KF296458 |
| *P. vasconiae* | CBS 339.79$^{T}$ | Soil, Spain | GU981599 | GU981653 | MN969309 | MN969144 |
| *P. vickeryae* | BRIP 72552a$^{T}$ | Soil, Australia | OP903479 | OP921966 | – | OP921965 |
| *P. viridissimum* | CGMCC 3.18796$^{T}$ | Acidic soil, China | KY495004 | KY495113 | MN969339 | KY495059 |
| *P. wotroi* | CBS 118171$^{T}$ | Leaf litter, Colombia | GU981591 | GU981637 | MN969313 | KF296460 |
| ***P. tibetense*** | **CGMCC 3.28597$^{T}$ = XZ5-3** | **Rhizosphere soil, Tibet, China** | **PQ643284** | **PQ519857** | **PQ519858** | **PQ519859** |
| *P. yuyongnianii* | CGMCC 3.25187$^{T}$ | Soil, China | OQ870820 | OR051175 | OR051352 | OR051499 |
| *P. zonatum* | CBS 992.72$^{T}$ | Soil, USA | GU981581 | GU981651 | MN969315 | KF296461 |

strap replicates with the best partition scheme and substitution model selected using ModelFinder (Kalyaanamoorthy et al. 2017). BI phylogenies were run in MrBayes v. 3.2.7 (Ronquist et al. 2012). Best fit models were selected according to the Akaike information criterion (AIC) using MrModeltest v. 2.4 (Nylander 2004). Posterior probabilities (PP) were estimated using Markov Chain Monte Carlo (MCMC) sampling, set to run for 1,000,000 generations with the average standard deviation of split frequencies less than 0.01 as the stopping criterion. In cases where this threshold was not achieved, the run was continued until the condition was met. Additionally, the initial 25% of the generated trees were discarded as burn-in.

## Results

### Morphology

Two novel species, *Penicillium lentum* and *P. tibetense*, were introduced within the sections *Brevicompacta* and *Lanata-Divaricata*, respectively, based on comprehensive phylogenetic analyses. General morphological characteristics and ecological information for the species included in these sections are provided in Table 2. Both newly described species exhibited morphological traits consistent with their respective sections. Specifically, *P. lentum* displayed limited growth with dense colonies on agar media and primarily produced terverticillate conidiophores. In contrast, *P. tibetense* demonstrated rapid growth on agar media, particularly exhibiting robust development on CYA at 30 °C, and predominantly formed biverticillate conidiophores. The morphological features of the new species and their closely related species are summarized in Table 3.

**Table 2.** Morphological and ecological data pertaining to the sections of the new species in this study.

| Section | Morphology | Ecology | References |
|---|---|---|---|
| *Brevicompacta* | Colonies restricted (occasionally moderately fast), texture velutinous; conidiophores terverticillate or multiramulate branched with wide stipes, smooth-walled. | Mainly soil and foods, also on plant leaves and rotting wood. | (Houbraken and Samson 2011; Frisvad et al. 2013; Wang and Wang 2013; Houbraken et al. 2020) |
| *Lanata-Divaricata* | Colonies grow rapidly, occasionally moderately fast; conidiophores monoverticillate, biverticillate or divaricate, occasionally terverticillate. | Commonly found in soil, also on rotting leaf litter and vegetable. | (Houbraken and Samson 2011; Houbraken et al. 2020) |

**Table 3.** Morphological features of new species and their closely related taxa.

| Species | Growth rates (mm) | | | Conidiophores branching | Cleistothecia /sclerotia | Conidia | | | Acid production on CREA |
|---|---|---|---|---|---|---|---|---|---|
| | CYA | CYA 30 °C | CYA 37 °C | | | Size | Shape | Roughening | |
| ***P. lentum*** | 7–10 | No growth | No growth | Terverticillate, sometimes biverticillate | Absent | 2–3 × 1.5–2.5 µm | Broadly ellipsoidal | Smooth | Absent |
| *P. tularense*[a] | n.a. | n.a. | n.a. | Asymmetric and divaricate | Cleistothecia | 2.2–2.6 µm | Globose to subglobose | Smooth | n.a. |
| ***P. tibetense*** | 42–50 | 42–52 | 21–27 | Biverticillate | Absent | 1.5–3 µm | Globose to subglobose | Finely rough | Absent |
| *P. excelsum*[b] | 35–50 | n.a. | 8–22 | Biverticillate, sometimes terverticillate | Absent | 4–5 × 2–3.2 µm | Ellipsoidal | Smooth | Absent |

[a]Description based on Paden (1971), [b]Description based on Taniwaki et al. (2016).

## Phylogenetic analyses

A BLAST search revealed that strain CGMCC 3.28596 is most closely related to *Penicillium tularense* (Identities: ITS: 97.52%, *BenA*: 81.13%, *CaM*: 84.91%, *RPB2*: 91.00%) within section *Brevicompacta*, and strain CGMCC 3.28597 exhibits the highest similarity to *P. excelsum* (Identities: ITS: 98.64%, *BenA*: 94.37%, *CaM*: 89.66%, *RPB2*: 94.84%) within section *Lanata-Divaricata*.

### Section *Brevicompacta*

The analyses of the concatenated dataset (*BenA*, *CaM*, and *RPB2*) comprised 20 predominantly ex-type strains, each with a total sequence length of 1876 bp (*BenA*: 469 bp, *CaM*: 512 bp, *RPB2*: 895 bp). Phylogenetic analyses divided section *Brevicompacta* into four distinct clades, with the new species *Penicillium lentum* forming a robustly supported clade alongside *P. tularense* (100% bs, 1.00 pp) (Fig. 1). In the phylogenetic analyses of individual genes, the new species, together with *P. tularense*, consistently formed a well-supported clade, mostly with high support values (>97% bs, 1.00 pp), except for ITS (Fig. 2).

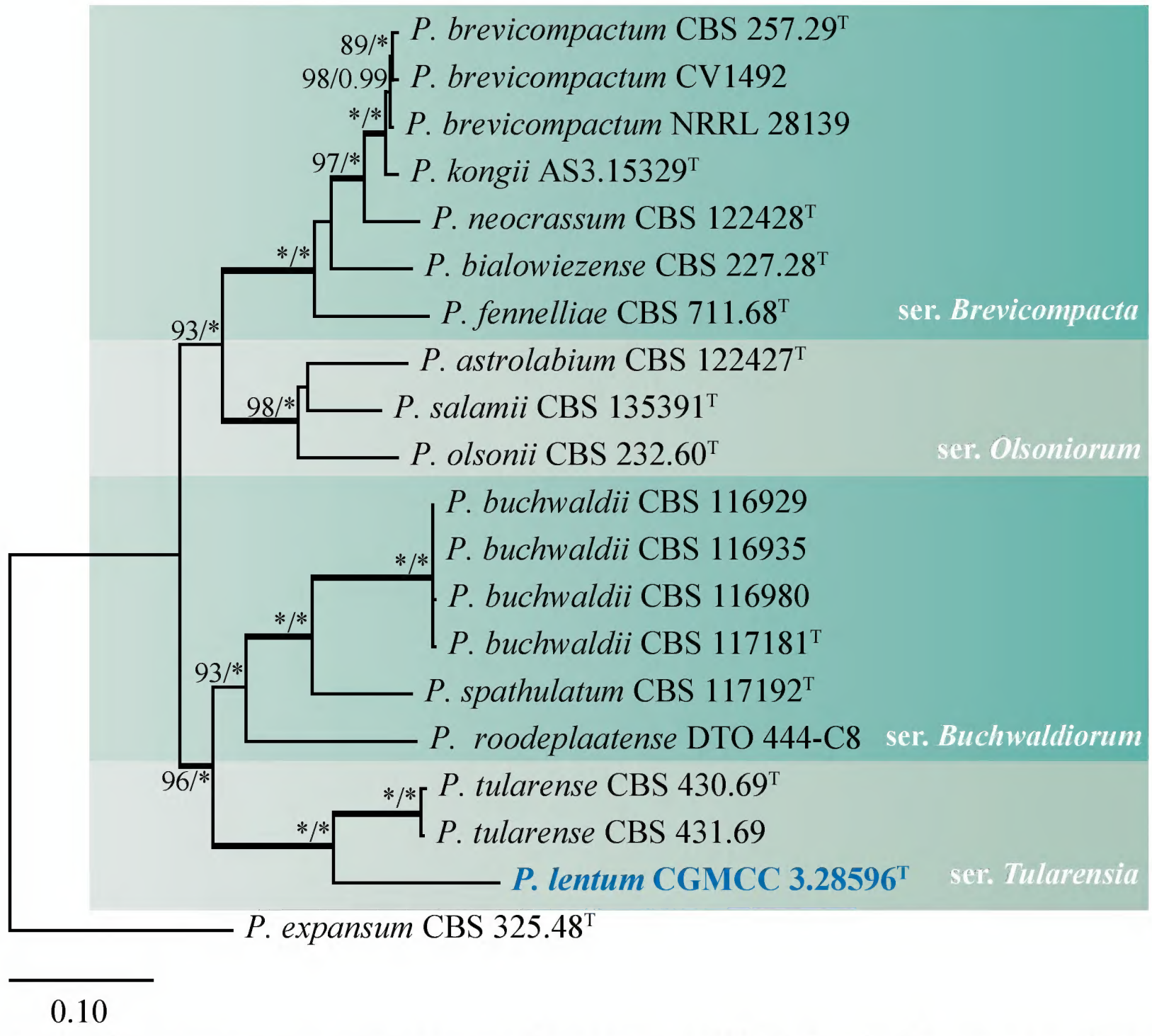


**Figure 1.** ML tree based on the concatenated data set (*BenA*, *CaM*, and *RPB2*) of section *Brevicompacta*. *Penicillium expansum* CBS 325.48T was designated as the outgroup. Nodes display bootstrap values (bs) exceeding 70% or posterior probabilities (pp) greater than 0.95. Branches with bs of 95% or higher and pp of 1.00 are depicted in bold. The strain described as the new species *P. lentum* is indicated with blue text. * Indicates bs = 100% or pp = 1.00, T = ex-type strain.

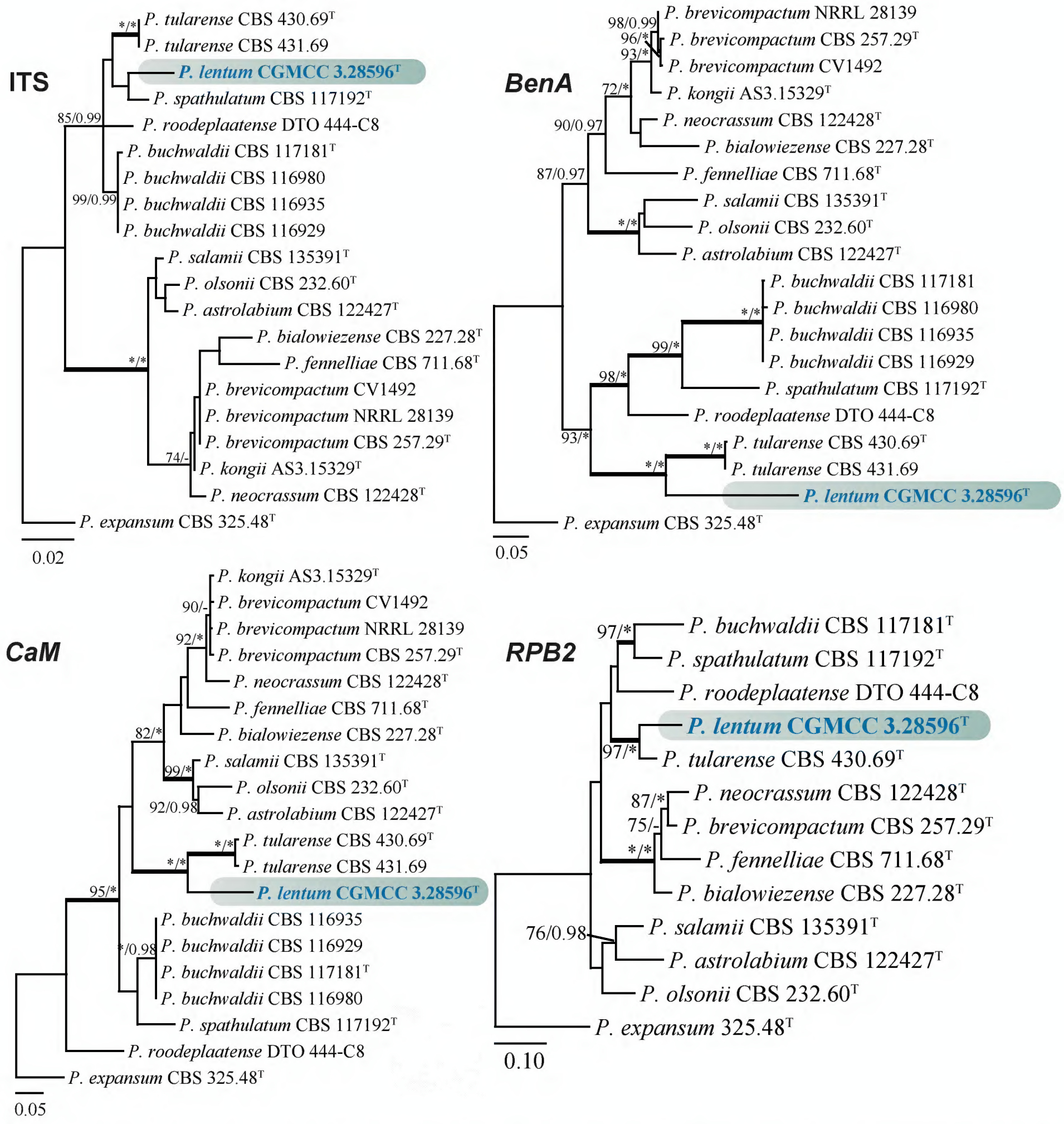


**Figure 2.** ML trees for section *Brevicompacta* based on ITS, *BenA*, *CaM*, and *RPB2*. *Penicillium expansum* CBS 325.48$^{T}$ was designated as the outgroup. Nodes display bootstrap values (bs) exceeding 70% or posterior probabilities (pp) greater than 0.95. Branches with bs of 95% or higher and pp of 1.00 are depicted in bold. The strain described as the new species *P. lentum* is indicated with blue text. * Indicates bs = 100% or pp = 1.00, $^{T}$ = ex-type strain.

## Section *Lanata-Divaricata*

In this section, we selected the series *Simplicissima*, *Dalearum*, and *Rolfsiorum*, comprising 71 predominantly ex-type strains, for phylogenetic analyses based on the concatenated dataset totaling 1876 bp (*BenA*: 504 bp, *CaM*: 617 bp, *RPB2*: 755 bp). The resulting phylogenies revealed that *Penicillium tibetense* is closely related to *P. excelsum* (64% bs, 0.97 pp; not depicted in Fig. 3). However, the significant evolutionary divergence observed supports the recognition of

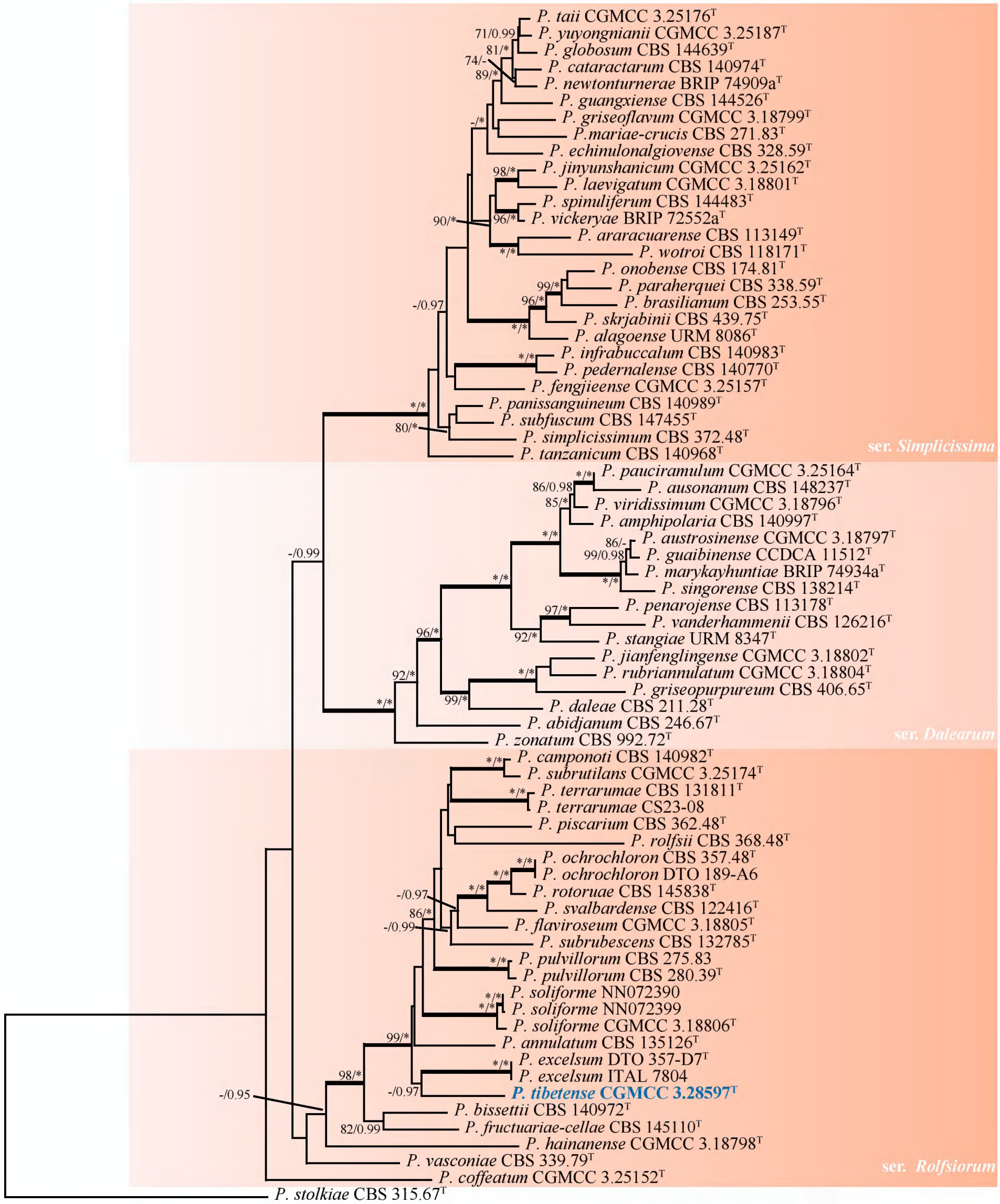


**Figure 3.** ML tree based on the concatenated data set (*BenA*, *CaM*, and *RPB2*) of section *Lanata-Divaricata* (series *Simplicissima*, *Dalearum*, and *Rolfsiorum*). *Penicillium stolkiae* CBS 315.67$^{T}$ was designated as the outgroup. Nodes display bootstrap values (bs) exceeding 70% or posterior probabilities (pp) greater than 0.95. Branches with bs of 95% or higher and pp of 1.00 are depicted in bold. The strain described as the new species *P. tibetense* is indicated with blue text. * Indicates bs = 100% or pp = 1.00, $^{T}$ = ex-type strain.

*P. tibetense* as a distinct species (Fig. 3). Phylogenetic analyses of individual genes within series *Rolfsiorum* demonstrated generally weak clustering support, with variations observed among the ITS, *BenA*, *CaM*, and *RPB2* datasets. Furthermore, *P. ochrochloron* and *P. rotoruae* share identical ITS sequences, making them indistinguishable through ITS phylogeny alone (Fig. 4).

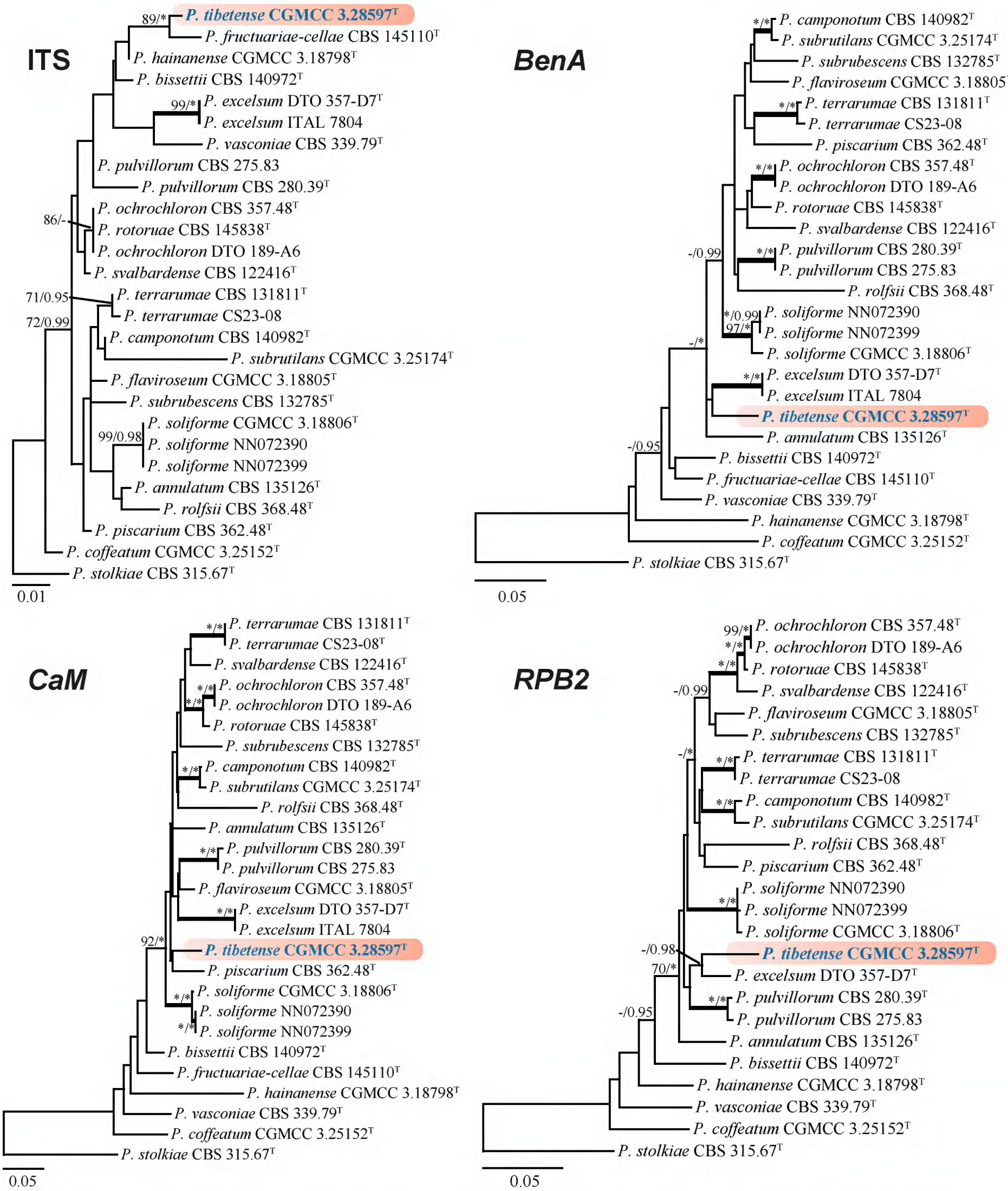


**Figure 4.** ML trees for section *Lanata-Divaricata* series *Rolfsiorum* based on ITS, *BenA*, *CaM*, and *RPB2*. *Penicillium stolkiae* CBS 315.67$^{T}$ was designated as the outgroup. Nodes display bootstrap values (bs) exceeding 70% or posterior probabilities (pp) greater than 0.95. Branches with bs of 95% or higher and pp of 1.00 are depicted in bold. The strain described as the new species *P. tibetense* is indicated with blue text. * Indicates bs = 100% or pp = 1.00, $^{T}$ = ex-type strain.

## Taxonomy

***Penicillium lentum* R.N. Liang & G.Z. Zhao, sp. nov.**
MycoBank No: 857346
Fig. 5

**Infrageneric classification.** Subgenus *Penicillium*, section *Brevicompacta*, series *Tularensia*.

**Etymology.** The specific epithet "*lentum*" is derived from lentus (Latin), reflecting the slow growth rate characteristic of this species.

**Type.** CHINA • Beijing, Haidian District, Beijing Forestry University, 40°0'20"N, 116°20'51"E, from indoor dust, 1 February 2024, collected by G.Z. Zhao, B24 (holotype HMAS 353385, dried culture; culture ex-type CGMCC 3.28596).

**Colony diameter after 7 d (mm).** CYA 7–10; CYA 30 °C, 37 °C no growth; MEA 6–9; YES 9–13; DG18 7–11; CREA 3.5–5.

**Colony characteristics (7 d).** CYA at 25 °C: Colonies deep, raised at center, margins low, narrow, irregular; mycelium white; texture velutinous, floccose areas present; sporulation moderate to good, conidia antique green (R. Pl. VI); exudate clear; reverse capucine buff (R. Pl. III); soluble pigment absent. MEA at 25 °C: Colonies deep, raised at center, margins low, narrow, entire; mycelium white; texture velutinous, floccose areas present; sporulation moderate to good, conidia celandine green (R. Pl. XLVII) to deep turtle green (R. Pl. XXXII); exudate clear; reverse light orange-yellow (R. Pl. III); soluble pigment absent. YES at 25 °C: Colonies deep, radially and concentrically sulcate, raised at center, margins low, narrow, entire; mycelium white; texture velutinous and fasciculate; sporulation good to strong, conidia glaucous-green (R. Pl. XXXIII); exudate absent; reverse cinnamon (R. Pl. XXIX); soluble pigment absent. DG18 at 25 °C: Colonies low, plane, margins low, wide, entire; mycelium white; texture velutinous and fasciculate; sporulation good, conidia bluish gray-green (R. Pl. XLII); exudate absent; reverse antimony yellow (R. Pl. XV); soluble pigment absent. CREA at 25 °C: Weak growth, no acid production. Ehrlich reaction negative.

**Micromorphology.** ***Conidiophores*** biverticillate to terverticillate; ***stipes*** smooth-walled, 70–236.5 × 2.5–4.5 µm; ***rami*** two when present, 6.5–18 × 2–4 µm; ***metulae*** divergent, 2–4 per branch/ramus, 4.0–13.0 × 2.5–4.5 µm; ***phialides*** ampulliform, 3–8 per metula, 4.5–8.0 × 2–3 µm; ***conidia*** broadly ellipsoidal, smooth-walled, 2–3 × 1.5–2.5 µm.

**Notes.** *Penicillium lentum* belongs to section *Brevicompacta* and is most closely related to *P. tularense* (Fig. 1). *Penicillium tularense* produces light brown to pale tan cleistothecia, which are not found in the new species (Paden 1971). Additionally, *P. lentum* has broadly ellipsoidal conidia, while *P. tularense* produces globose to subglobose conidia (Table 3).

***Penicillium tibetense* R.N. Liang & G.Z. Zhao, sp. nov.**
MycoBank No: 857347
Fig. 6

**Infrageneric classification.** Subgenus *Aspergilloides*, section *Lanata-Divaricata*, series *Rolfsiorum*.

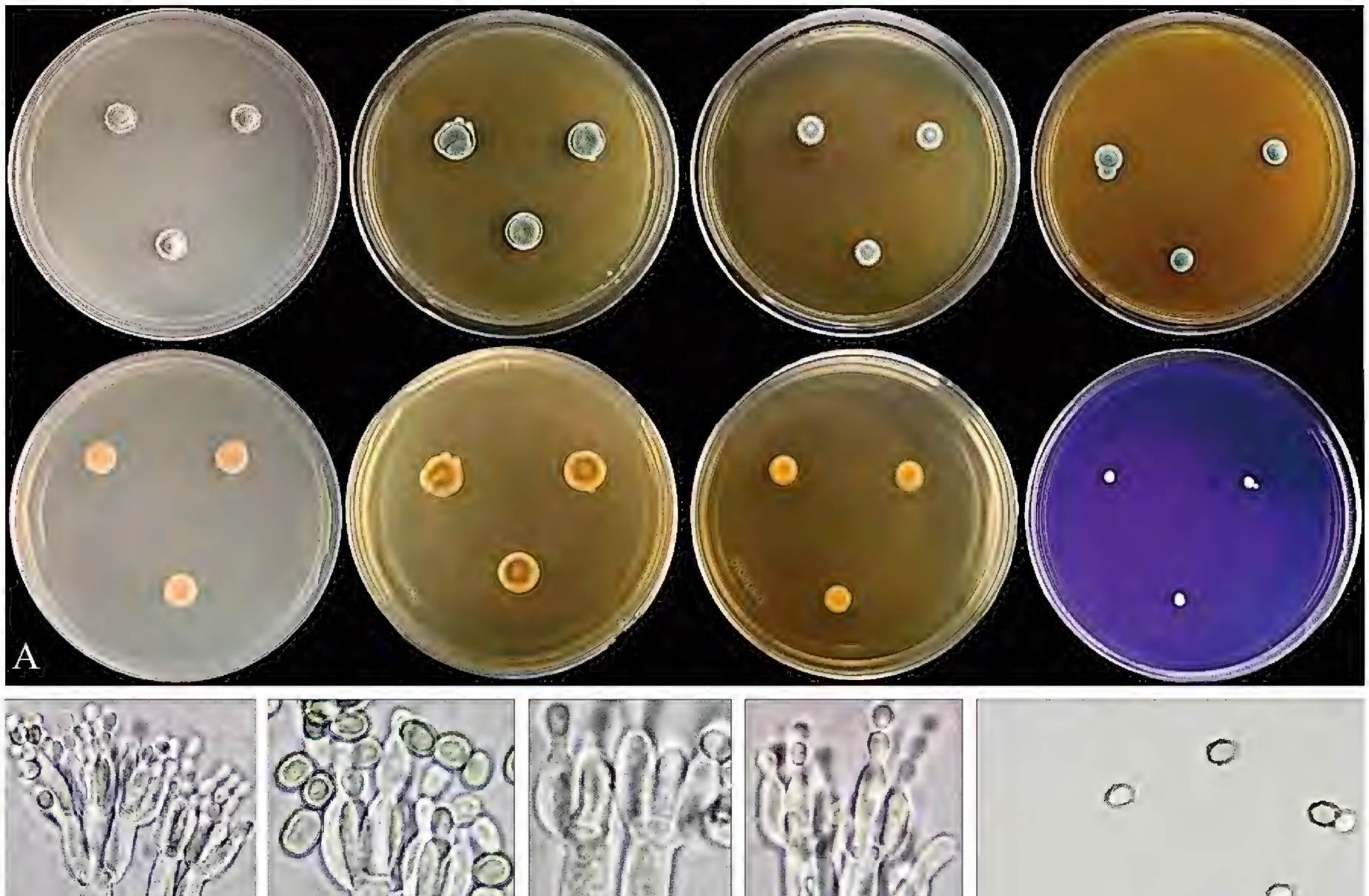


**Figure 5.** *Penicillium lentum* CGMCC 3.28596. **A** Colonies on medium at 25 °C for 7d (left to right, top row: CYA, YES, DG18, MEA obverse; second row: CYA reverse, YES reverse, DG18 reverse, CREA obverse) **B–E** conidiophores **F** conidia **G–I** SEM micrograph of conidiophores **J** SEM micrograph of conidia. Scale bars: 10 μm (**B–I**); 2 μm (**J**).

**Etymology.** The specific epithet "*tibetense*" denotes the geographical origin of the species, indicating its discovery in Tibet.

**Type.** China • Tibet, Changdu City, Basu County, Kangyu Tunnel, 30°33'53"N, 96°15'25"E, from rhizosphere soil of grasses, 19 July 2023, collected by X.W. Peng, XZ5-3 (holotype HMAS 353386, dried culture; culture ex-type CGMCC 3.28597).

**Figure 6.** *Penicillium tibetense* CGMCC 3.28597. **A** Colonies on medium at 25 °C for 7d (left to right, top row: CYA, YES, DG18, MEA obverse; second row: CYA reverse, YES reverse, DG18 reverse, CREA obverse) **B–D** conidiophores **E** conidia **F, G** SEM micrograph of conidiophores **H** SEM micrograph of conidia. Scale bars: 10 μm (**B–G**); 2 μm (**H**).

**Colony diameter after 7 d (mm).** CYA 42–50; CYA 30 °C 42–52; CYA 37 °C 21–27; MEA 48–52; YES 46–52; DG18 20–26; CREA 24–26.

**Colony characteristics (7 d).** CYA at 25 °C: Colonies low to moderately deep, radially sulcate, margins low, narrow, entire; mycelium white; texture floccose;

sporulation moderate, conidia livid pink (R. Pl. XXVII); exudate clear; reverse light purple-drab (R. Pl. XLV) to avellaneous (R. Pl. XL); soluble pigment absent. CYA at 30 °C: Colonies low to moderately deep, radially sulcate, margins low, narrow, entire; mycelium white; texture floccose; sporulation moderate, conidia livid pink (R. Pl. XXVII); exudate clear; reverse brownish vinaceous (R. Pl. XXXIX); soluble pigment absent. CYA at 37 °C: Colonies moderately deep, radially sulcate, margins low, narrow, entire; mycelium white; texture floccose; sporulation sparse, conidia livid pink (R. Pl. XXVII); exudate clear; reverse light buff (R. Pl. XV); soluble pigment absent. MEA at 25 °C: Colonies low to moderately deep, radially sulcate, margins low, narrow, entire; mycelium white; texture floccose; sporulation sparse to moderate, conidia pale brownish vinaceous (R. Pl. XXXIX); exudate clear; reverse antimony yellow (R. Pl. XV); soluble pigment absent. YES at 25 °C: Colonies moderately deep, randomly sulcate, margins low, wide, entire; mycelium white; texture floccose; sporulation moderate, conidia antique green (R. Pl. VI); exudate clear; reverse antimony yellow (R. Pl. XV); soluble pigment absent. DG18 at 25 °C: Colonies low, radially sulcate, margins low, wide, entire; mycelium white; texture floccose; sporulation sparse, conidia ecru-drab (R. Pl. XLVI); exudate absent; reverse orange-pink (R. Pl. II); soluble pigment absent. CREA at 25 °C: Strong growth, no acid production. Ehrlich reaction negative.

**Micromorphology.** ***Conidiophores*** biverticillate; ***stipes*** finely rough-walled, 27–364.5 × 2–3 µm; ***metulae*** appressed to divergent, 2–4 per stipe, 8–15 × 1.5–3 µm; ***phialides*** ampulliform to cylindrical, 2–6 per metula, 5–10.5 × 1.5–3 µm; ***conidia*** globose to subglobose, finely rough-walled, 1.5–3 µm diam.

**Notes.** *Penicillium tibetense* is classified in section *Lanata-Divaricata* and exhibits a close phylogenetic relationship to *P. excelsum* (Fig. 3). This novel species generates globose to subglobose, finely rough-walled conidia that distinguish it from *P. excelsum* (Table 3). Additionally, *P. tibetense* demonstrates more robust growth on CYA at 37 °C compared to *P. excelsum* (21–27 mm vs. 8–22 mm) (Taniwaki et al. 2016).

## Discussion

*Penicillium*, a ubiquitous and diverse fungal genus, plays pivotal roles in natural ecosystems while maintaining substantial economic importance and significant relevance to human affairs. The recent rapid increase in newly described species within this genus suggests that numerous taxa remain undiscovered. Given the extensive biotechnological applications of *Penicillium* species, accurate taxonomic identification is paramount, necessitating comprehensive species delineation through polyphasic approaches. In the present study, we introduced two novel species: one belonging to section *Brevicompacta* and the other to section *Lanata-Divaricata*.

Section *Brevicompacta* currently comprises 15 species distributed across four series (Visagie et al. 2024a, 2024b) and is represented in our findings by the newly described *P. lentum* sp. nov. This species, classified within series *Tularensia*, is characterized by predominantly terverticillate conidiophores and demonstrates a close relationship with other members of section *Brevicompacta* (Table 2). Section *Lanata-Divaricata* is characterized by its remarkable species diversity and rapid colony growth, primarily comprising soil-inhabiting

species, with over 90 taxa currently recognized across five series (Houbraken et al. 2020; Visagie et al. 2024b). The newly identified *Penicillium tibetense* assigned to series *Rolfsiorum* exhibits characteristic rapidly expanding colonies and produces biverticillate conidiophores, consistent with the morphological features typical of this series. Members of section *Lanata-Divaricata* are ecologically significant as decomposers of organic matter (Lichtner et al. 2022), with notable biotechnological potential exemplified by *P. subrubescens*, which has demonstrated efficient inulinase production (Mansouri et al. 2013).

Phylogenetic analyses of section *Brevicompacta* demonstrated that our strain *P. lentum* formed a well-supported clade with its closest relative, *P. tularense* (Fig. 1), a relationship corroborated by shared morphological characteristics such as conidiophore branching patterns and growth rates. However, our strain could be clearly distinguished from *P. tularense* based on distinct phenotypic features, including the presence or absence of cleistothecia and differences in conidial morphology (Table 3). The phylogenetic relationships within section *Lanata-Divaricata* remain unresolved, primarily due to the poor support values in certain clades (Houbraken et al. 2020), exemplified by a clade comprising *P. camponoti*, *P. piscarium*, *P. rolfsii*, *P. subrutilans*, and *P. terrarumae* (Fig. 3), which highlights the persistent challenges in resolving certain taxonomic groups even with multigene phylogenetic approaches.

To address these limitations, we recommend expanding the taxonomic sampling to include strains from diverse geographical origins and ecological niches. This strategy would not only generate additional reference sequences but also facilitate the discovery of novel species and the detection of infraspecific variation (Visagie and Houbraken 2020). Furthermore, sequencing additional gene regions represents a promising approach to enhance phylogenetic resolution (Visagie et al. 2021). The rapid development of high-throughput sequencing technologies has resulted in an accelerated increase in genomic data availability (Kapli et al. 2020), positioning phylogenomics as an essential tool in modern fungal taxonomy and systematics. By leveraging genome-scale data, phylogenomics is poised to overcome the limitations of single gene or multigene analyses, providing robust statistical support for clade resolution and enabling the reconstruction of a highly resolved fungal tree of life (Burki et al. 2020; Zhou and May 2023). These advancements underscore the transformative potential of phylogenomics in addressing long-standing taxonomic challenges and refining our understanding of fungal evolutionary relationships.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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## Author contributions

Rui-Na Liang: Formal analysis, investigation, data curation, writing – original draft preparation, visualization; Xiang-Hao Lin and Miao-Miao An: Investigation, visualization; Guo-Zhu Zhao: Conceptualization, methodology, validation, resources, writing – review and editing, supervision, funding acquisition. All authors have read and agreed to the published version of the manuscript.

## Data availability

All of the data that support the findings of this study are available in the main text. All sequences generated in this study have been submitted to GenBank.

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